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Ectomycorrhizal fungi drive positive phylogenetic plant–soil feedbacks in a regionally dominant tropical plant family

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Abstract. While work in temperate forests suggests that there are consistent differences in plant–soil feedback (PSF) between plants with arbuscular and ectomycorrhizal associations, it is unclear whether these differences exist in tropical rainforests. We tested the effects of mycorrhizal type, phylogenetic relationships to overstory species, and soil fertility on the growth of tree seedlings in a tropical Bornean rainforest with a high diversity of both ectomycorrhizal and arbuscular mycorrhizal trees. We found that ectomycorrhizal tree seedlings had higher growth in soils conditioned by close relatives and that this was associated with higher mycorrhizal colonization. By contrast, arbuscular mycorrhizal tree seedlings generally grew more poorly in soils conditioned by close relatives. For ectomycorrhizal species, the phylogenetic trend was insensitive to soil fertility. For arbuscular mycorrhizal seedlings, however, the effect of growing in soils conditioned by close relatives became increasingly negative as soil fertility increased. Our results demonstrate consistent effects of mycorrhizal type on plant–soil feedbacks across forest biomes. The positive effects of ectomycorrhizal symbiosis may help explain biogeographic variation across tropical forests, such as familial dominance of the Dipterocarpaceae in southeast Asia. However, positive feedbacks also raise questions about the role of PSFs in maintaining tropical diversity.

Key words: biodiversity; conspecific negative density dependence; Dipterocarpaceae; Janzen-Connell; mycorrhizal fungi; natural enemies; soil fertility.

Introduction

Localized accumulation of species-specific natural enemies has been hypothesized to influence the diversity and structure of plant communities by limiting conspecific recruitment and thereby preventing competitive exclusion by dominant species (Janzen 1970, Connell 1971). While the original Janzen-Connell framework focused primarily on herbivorous arthropods and seed predators, soil-borne microorganisms are also important natural enemies that strongly influence seedling recruitment (Augspurger 1983, Bever et al. 1997, Gilbert 2002, Mangan et al. 2010*a*). Experiments measuring plant growth in soils conditioned by conspecifics often show more negative effects of microbes compared with soils conditioned by heterospecifics, an effect known as negative plant soil feedbacks (PSFs) (Bever et al. 1997, Mangan et al. 2010*a*). Because of their potential role in causing conspecific negative density-dependence (CNDD), PSFs can shape plant species' population dynamics and community structure (Condit et al. 1992, van der Heijden et al. 1998, Klironomos 2002, Comita et al. 2010, Bagchi et al. 2010*a*, 2014, Mangan et al. 2010*b*, Johnson et al. 2012).

Despite the potential importance of negative PSFs in maintaining diversity in tropical forests, recent evidence has shown that the strength and direction of PSFs can vary dramatically (De Long et al. 2018). For example, PSFs ranged from positive to negative between co-occurring tree species (Bennett et al. 2017), and the same tree species have been shown to vary in PSF strength across sites (Liu et al. 2015, Kivlin et al. 2018). One likely reason for this variation is that co-occurring plant species often host distinct suites of specialized symbiotic microbes (Duhamel et al. 2019). Mycorrhizal fungi are perhaps the most common form of variation in plant–microbe symbiosis, with 67% and 31% of trees forming host-specific associations with either ectomycorrhizal (EM) or arbuscular mycorrhizal (AM) fungi, respectively, in a global forest inventory data set (Steidinger et al. 2019). A number of functional differences exist between EM and AM fungi, including host specificity, dispersal ability, enzymatic capacities, pathogen protection, and effects on the overall soil microbiota (Bruns and Shefferson 2004, Morris et al. 2007, Hoeksema

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et al. 2010), that could lead to variation in PSF strength (Bennett et al. 2017, Teste et al. 2017). Indeed, a landmark study by Bennett et al. (2017) found that EM trees in temperate North America generally experienced a positive effect of home soil microbes (i.e., positive PSF) while AM trees generally experienced a negative effect of home soil microbes (i.e., negative PSF). Similarly, a recent field survey from subtropical China found that accumulation of EM fungi in the soil was correlated with reduction in CNDD strength (Chen et al. 2019). Despite these results, the generality of mycorrhizal effects on plant–soil interactions across the global diversity of forest types and abiotic conditions is not known. This knowledge is particularly important since positive PSF may act to reduce the capacity for species coexistence (Stump and Comita 2018) and has consequences for our understanding of global plant diversity.

One major reason for uncertainty in the generality of mycorrhizal effects on PSF is the paucity of experimental studies from tropical forests. While some studies have looked experimentally for the evidence of positive feedbacks in tropical EM tree species (e.g., McGuire 2007, Corrales et al. 2016), these studies have focused on single tree species that form monodominant stands that are outliers within otherwise mixed forests dominated by AM symbiosis (Janos 1980, Torti et al. 1997). However, EM symbiosis is common in some tropical rainforests, such as in Southeast Asia, where a diverse suite of EM trees can cumulatively account for ~40% of the basal area across a large extent of mixed forest (Proctor et al. 1983, Alexander and Hogberg 1986, Brearley 2012). Yet, no experimental studies of plant–soil feedback have been conducted using multiple tree species from mixed EM–AM tropical rainforests. Thus, whether consistent differences in PSF exist between dominant mycorrhizal host types in tropical rainforests has not been established experimentally at the community scale.

Soil conditions may also interact with mycorrhizal associations to generate variation in the outcome of plant–soil–microbe interactions. Interactions with symbiotic organisms are well known to vary with environmental context (Bronstein 1994). The beneficial effects of AM fungi have been shown to be particularly sensitive to the local soil environment, in some cases changing from mutualistic to parasitic on soil formations with high soil nutrient levels (Bronstein 1994, Johnson et al. 2010). Mycorrhizal fungi may also influence the local soil environment directly. EM fungi are often correlated with increased soil carbon and decreased mineral nitrogen (Phillips et al. 2013, Averill et al. 2014). This may create a competitive advantage for EM plants as EM fungi appear to have greater enzymatic capacity to access nutrients bound in the complex organic forms found in the plant litter of nutrient-depleted soil (Read and Perez-Moreno 2003, Lindahl and Tunlid 2014), but see (Pellitier and Zak 2017). Thus, the beneficial effects of mycorrhizal fungi on plant growth are likely to vary due to local biotic factors and underlying parent material that affects soil fertility. However, it is not clear whether this translates to systematic differences in the net PSF effect experienced by AM and EM plants across soil fertility gradients.

Plant species within a community also vary in how much overlap there is between the communities of microbes that accumulate in the soils they condition. Overstory trees can shape the soil microbial community encountered by a seedling via root exudates, litter chemistry, and the accumulation of host-associated mutualists and pathogens. Because traits such as litter chemistry and microbial associations can be evolutionarily conserved, the phylogenetic relationship between a seedling and the nearest overstory tree may predict whether such localized soil biota enhance or reduce seedling growth and/or survival, with potential consequences for community structure (Gilbert and Webb 2007, Liu et al. 2011). Experiments growing seedlings in soils with different inocula have shown that PSFs are more strongly negative when seedlings and the adult tree nearest the soil inoculum source are phylogenetically closely related (Bagchi et al. 2010*a*, Liu et al. 2011). However, PSFs measured in such experiments are the net outcome of not only the negative effects caused by soil pathogens, but also the positive effects of soil mutualists, which also may be more similar between more closely related species (Nara 2006, Ishida et al. 2007). As a result, the greater host specificity often associated with EM symbiosis (Bruns et al. 2002, Davison et al. 2015) may cause PSF to vary more strongly with evolutionary relatedness for EM, compared to AM host species.

To dissect these key sources of variation in PSF, we conducted a shadehouse experiment to test whether the growth of seedlings in field conditioned soils depends on a tree species' mycorrhizal type (EM vs. AM), the effects of shared evolutionary history on host specific soil microbes, and the associated soil conditions (i.e., differences in soil physical and chemical properties due to both host effects or underlying geological variation). Our study site is a high-diversity Bornean rain forest that is co-dominated by EM and AM tree species, and in which tree species composition varies strongly along a geologically driven soil fertility gradient (Davies et al. 2005). This system allowed us to experimentally test the effects of soil fertility (due to host effects and distinct soil formations) and mycorrhizal type on PSF in an ecologically meaningful context. Many studies calculate PSF as a ratio of the plant growth response in conspecific-conditioned soil to an average response across heterospecific-conditioned soils of unspecified phylogenetic distance from the focal species. However, this approach can obscure the very ecological variation in feedback effects that needs to be quantified in order to evaluate the capacity for PSF to affect species coexistence. Instead, to quantify this variation, we used a regression-based analysis of seedling growth across a range of phylogenetically defined soil conditioning environments, which facilitated generalization of PSF-

mediated seedling growth responses across the community of overstory trees present at our field site and allowed for consideration of realistic variation in soil nutrient availability. We predicted that (1) PSF trends in this forest would, on average, be negative, supporting negative PSF as a mechanism promoting floristic diversity, but that (2) this variation would be modified by mycorrhizal type and soil fertility. Specifically, we expected EM seedlings to experience less negative overall feedbacks from host specific microbes than AM seedlings, and that the abiotic environment would have a smaller effect on host specific plant–microbe interactions for EM seedlings than AM seedlings.

Methods

Study site

Lambir Hills National Park (LHNP) is a 7,800-ha protected area in northwest Borneo in Sarawak, Malaysia (4°20′ N, 113°50′ E). It is classified as tropical mixed dipterocarp forest (Lee et al. 2002). A 52-ha, long-term, forest dynamics plot located at this site (Lee et al. 2002) is characterized by two geological formations that produce a gradient of soil texture spanning coarse, infertile sandy loam to fine, less infertile clay soil (Baillie et al. 2006). Variation in tree species composition and dynamics in the plot is strongly structured by this edaphic fertility gradient (Davies et al. 2005, Russo et al. 2005). Over 1,200 tree species occur in the plot, with dominance by species of the EM Dipterocarpaceae, which account for approximately 16% of stems and 42% of basal area (Lee et al. 2002). Forest wide seed production occurs irregularly, separated by multi-year intervals in southeast Asian rainforests. We took advantage of a 2013 fruiting event to establish a seedling shadehouse experiment at LHNP. We used the well-described forest community variation along the edaphic gradient in the plot as the basis for our experimental design to separate the effects of mycorrhizal type, soil properties, and phylogenetic relatedness to overstory trees on seedling growth.

Experimental design

In order to understand the causes of variation in plant–soil–microbe interactions at LHNP, we established a shadehouse experiment using seeds collected after a 2013 general flowering event. Seedlings were grown in factorial combinations of soil treatments designed to manipulate the presence of host specific soil microbes (via phylogenetically structured field soil collections), variation in soil nutrient conditions (via geologically structured soil collections), and seedling mycorrhizal status (via collection of seeds from AM or EM tree species). To more precisely separate biotic and abiotic factors that influence seedling growth, our experimental design also included a factorial fungicide treatment as well as quantitative measurement of nutrients from each soil collection. Each experimental treatment is described in detail below and presented graphically in Fig. 1.

Manipulation of host specific microbes through phylogenetic based soil collection

In order to manipulate the presence of host specific microbes that might influence seedling growth, we grew seedlings of each focal species in soils collected from beneath adult trees that differed in their phylogenetic relatedness to the focal seedling species. To include a consistent range of phylogenetic distances, for each seedling species we collected soils from beneath adults that were conspecific, congeneric, confamilial, conordinal, or a different lineage (hetero-ordinal). We refer to these overstory trees hereafter as "conditioning species." Soil collections for each seedling species × phylogenetic combination were sourced from a single conditioning species. To better separate the effect of phylogenetic relatedness from mycorrhizal association, for each focal species, we included both a distantly related EM host soil source and a distantly related AM host soil source (hetero-ordinal in both cases). Hereafter we use the term "phylogenetic distance(s)" to refer to the soils collected from different conditioning species and "phylogenetic PSF" to refer to microbe-mediated growth effects that depend on the phylogenetic relatedness of the conditioning species to the focal species.

Manipulation of soil nutrients through geologically structured soil collections

In order to test the influence of soil resource availability on plant microbe interactions, our phylogenetically structured soil collections were crossed with the two primary soil formations at LHNP, sandy loam and clay, respectively, the low and high points of the local soil fertility gradient. Thus, for each seedling species, the phylogenetic distance gradient from congeneric to hetero-ordinal was replicated on lower and higher fertility soils. Because there are few generalist tree species that occur on both soils (Davies et al. 2005), soil inocula for each phylogenetic level were necessarily sourced from different species on sandy loam vs. clay soils (Appendix S1: Table S1). While we treated soil type categorically in our design and soil collection process to ensure we captured the local range of soil fertility, there is also important variation in fertility within soil types (e.g., due to overstory litter inputs or different conditioning tree species). To account for abiotic differences in soil nutrients due both to geology and tree species, for each soil collection from a given conditioning species, we measured starting supply rates of 14 plant-available anions and cations (see Appendix S1: Fig. S1). This was done for all soil collections and the corresponding fungicide addition treatments (see below), for a total of 31 conditioning species × 2 fungicide treatments = 62 soil collections. Soil nutrient supply was estimated using Plant Root Simulator (PRS) ion exchange resin membranes (Western Ag Innovations, Saskatoon,

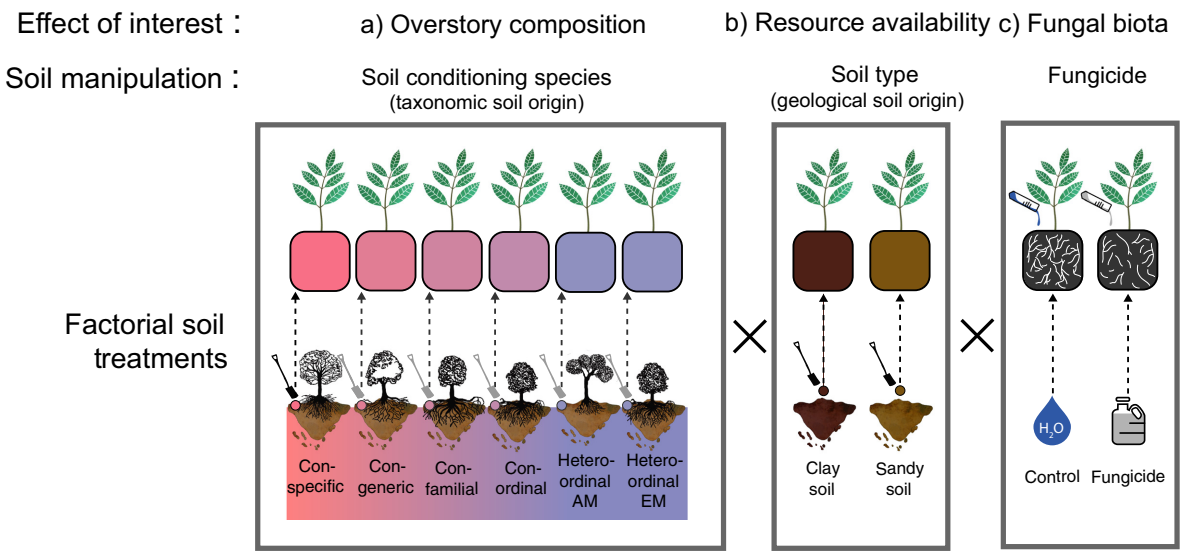

FIG. 1. Experimental design overview, illustrating the factorial experimental treatments used in the shadehouse experiment. The design manipulated (a) overstory composition: the presence of host-specific microbes by growing seedlings in soils collected from overstory trees ranging in phylogenetic relatedness from conspecific (pink) to hetero-ordinal (purple); (b) resource availability: the availability of soil nutrients by collecting soils from geological formations giving rise to two distinct soil types (sandy loam or clay), and (c) fungal biota: the activity of fungal pathogens and mutualists through the application of fungicide. This design was replicated for each of the three AM and five EM seedling focal7 species grown in the shadehouse experiment.

Saskatchewan, Canada). PRS probes were buried for 8 weeks in 2-L pots filled with a representative sample of each soil collection × fungicide treatment (without seedlings, as specified by the manufacturer), after which probes were removed, processed, and sent to the manufacturer for chemical analysis. This allowed us to use quantitative metrics of soil fertility in subsequent analyses rather than categorical effects.

Manipulation of host specific microbes through fungicide application

As an additional step to confirm the biotic nature of any effects on plant growth, we included a factorial fungicide treatment in our experiment. As all mycorrhizas and many key plant pathogens are fungal we assumed fungi are the primary drivers of host specific growth effects. To do this, we added a captan fungicide treatment such that half of all seedlings of each focal species in each soil type × phylogenetic distance treatment combination received fungicide. While fungicides are known to vary in their efficiency across fungal taxa, soil types, and non-target organisms (Bagchi et al. 2014), we chose Captan as a similar study from southeast Asia found that it effectively removed the effect of host specific soil pathogens (Liu et al. 2011).

Seed collection of AM and EM tree species

In order to test the effects of mycorrhizal association on plant–soil–microbe interactions, we collected seeds from AM and EM tree species between December 2013 and February 2014, following a general flowering event in the fall of 2013. Seeds were collected prior to or in very early stages of germination. We did not collect seeds if the emerged radicals had touched the litter on the forest floor. Seeds were not surface sterilized due to speed of germination (for most of the study species, seeds have no dormancy and germinate shortly after or immediately upon dropping) and concern that this would kill the seedlings. We washed seeds thoroughly to remove any soil, and then rinsed them in sterile water before placement into trays of commercially obtained washed river sand. Seeds germinated in January and February 2014. We were able to collect sufficient seeds from four dipterocarp EM hosts (*Dryobalanops aromatica*, *Shorea curtisii*, *Shorea laxa*, and *Shorea scaberrima*) and one species of Fagaceae (*Castanopsis hypophoenica*). The three focal AM host species (*Dacryodes expansa*, *Whiteodendron moultonianum*, and *Madhuca utilis*) were from three different families, Burseraceae, Myrtaceae, Sapotaceae, respectively. In total, our experiment consisted of 1,127 seedlings with 3–10 seedlings per treatment combination. Variation in the final number of replicates between seedling species (8 seedling species × 5–6 soil phylogenetic distances (soil conditioning species) per species × 2 soil types × 2 fungicide groups × 3–10 replicates = 1,127) (Appendix S1: Table S2) was due to variability in seed production and our ability to source soil treatments.

Field soil collection methods

We collected soils to be used as inoculum for the PSF treatments from one to three source trees per

conditioning species. Because of the possible disturbance involved we did not collect soils from within the Lambir Forest Dynamics Plot (where all stems >5 cm have been mapped and inventoried), and thus were constrained by our ability to locate and identify tree species in the adjacent forest, which has not been mapped and inventoried. Vouchers for all tree species used for soil collection are kept in the Lambir Forest Dynamics Plot herbarium (a list of all soil collections is in Appendix S1: Table S1). Soils were collected within 2 m from the trunk of each source tree and at multiple locations around the base of the tree when possible. Leaf litter was cleared from collection sites, and soil pits were dug to a depth of up to 30 cm using a shovel sterilized with 70% ethanol. All soils from each pit were sieved through baskets with 3 × 10 mm mesh size to remove rocks and large roots, and to homogenize particle size, but the coarse mesh allowed fine root fragments and other sources of microbial inoculum to persist. Soils collected from a given conditioning species were pooled, thoroughly homogenized, and subsequently mixed 1:1 with commercially obtained sand to improve drainage. Soils were processed and mixed within 24 h of collection from the field, and 2 L of the live soil/sand mixture was used per seedling.

While there has been recent discussion critiquing the common use of pooled inoculum (mixed soil samples) in plant soil feedback studies (Reinhart and Rinella 2016, Rinella and Reinhart 2017) there is lack of broad consensus against this method and the only empirical comparison of mixed soil sample and independent soil sample approaches to date found no influence on study outcomes (Gundale et al. 2019). As a result, the use of mixed soil samples in our study is unlikely to affect our results or their interpretation.

Seedling establishment and measurements

In February and March of 2014, seedlings were transplanted from germination trays into soil mixtures in 2 L polyethylene pots in the shadehouse. Transplanting into soil mixtures took place within three days of live soil collection. Seedlings were allowed to establish for 10 d, during which time they were replaced if they suffered transplant mortality. At 10 d after transplant, we measured two stem diameters at a marked point on the stem near the base of the seedling, height from the marked point to the apical meristem, and leaf number for all seedlings in order to estimate initial biomass. All seedlings were kept well-watered throughout the duration of the experiment, using rainwater from a catchment system to avoid unintentional introduction of soil organisms or sediment by the local water source, which is stream fed. In the shadehouse, seedlings were arranged in experimental blocks.

For each focal species, seedlings were distributed at random among 16 nursery benches, ensuring that treatment combinations were distributed evenly. Whole benches were designated either for control (non-fungicide) or fungicide treatment, alternating control and fungicide benches inside the shadehouse to avoid drift during fungicide application. Pairs of adjacent control and fungicide benches were designated as experimental blocks, with a total of eight experiment blocks. From 10 days after transplant until the end of the experiment, seedlings designated for fungicide treatments were given a Captan application fortnightly, consisting of a soil drench in aliquots of 50 mL/individual at a rate of 0.66 g/L following (Liu et al. 2011). All control plants received a 50 mL "mock treatment" of water at the same interval. Captan is a metalaxyl-based broad-spectrum fungicide, which acts on a wide range of soil fungi including both Oomycete and fungal pathogens (Cohen and Coffey 1986, Barberá 1989, Martınez-Toledo et al. 1998).

Seedling harvest

Seedlings were harvested between mid-February and June 2015, and ranged from 325 to 453 d old. All tissues were separated and oven dried at 60°C for at least 72 h before weighing to an accuracy of 0.0001 g to obtain the biomasses of leaves, stems, coarse, and fine roots, and total plant biomass. To develop allometric equations for estimation of initial biomass of experimental seedlings, the same data were collected for a subset of 6–20 seedlings (depending on seed availability) of each focal species harvested at the beginning of the experiment (Appendix S1: Table S3).

Fresh roots of all EM host species (*Dryobalanops*, *S. curtisii*, *S. laxa*, *S. scaberrima*, *Castanopsis*) were inspected for ECM colonization at harvest using a 10× dissecting microscope. We estimated percent colonization by counting approximately 100 root tips from 10 ~1-cm root fragments sampled randomly from the root system of each seedling and scoring each tip as either colonized or uncolonized. Estimates of colonization were made immediately following root washing, and root fragments used were returned to the root system before further processing. Field conditions prevented us from estimating AM colonization, which requires additional staining procedures and higher magnification microscopy. While we retained dried roots for AM staining, import permit restrictions have prevented us from examining them.

Data analysis

To determine the primary factors that influence the outcome of plant–microbe interactions, we developed statistical models to test the effect on plant growth of our four experimental variables: mycorrhizal association (factor with two levels), phylogenetic distance (continuous), soil fertility (continuous), and fungicide application (factor with two levels). Calculation of continuous variables and model design are explained in more detail in *Statistical modeling*.

Phylogenetic tree assembly and seedling–soil phylogenetic distance

In order to quantify how evolutionary history influences plant response to host specific microbes, we first estimated evolutionary relationships among tree species used in this study by assembling a phylogenetic tree of all plant taxa used either as seedlings in the growth experiment or soil conditioning species (Methods S1). To ease interpretation seedling–soil phylogenetic distances were relativized by the maximum distance within each focal species (361 million years ago, for all species) to give a relative phylogenetic distance measurement ranging from 0 (conspecific) to 1 (distantly related; Liu et al. 2011).

This phylogenetic approach differs from traditional PSF approaches (e.g., Mangan et al. 2010) by defining plant soil feedbacks as a trend in seedling performance across a gradient of soils with respect to the phylogenetic distance between the focal seedling species and the conditioning adult species, rather than comparing growth in home vs. away soils. Second, rather than examining response ratios, we measured response directly in terms of plant growth. This is facilitated by our phylogenetic design and allowed us to (1) examine plant responses using a more intuitive metric, (2) avoid the artificial loss of variance associated with using average growth on conspecific soils to calculate response ratios, and (3) to explicitly consider interactions with realistic variation in soil fertility. Additionally, to the extent that evolutionary relationships influence the degree to which species share both pathogens and mutualists, phylogenetic analysis can help to predict the range of possible growth feedbacks a seedling may experience in a diverse tree community. While this approach is somewhat different than that used in other PSF studies, our approach is measuring the same underlying phenomenon (i.e., differences in the effect of soil microbes on plant growth) and thus for the purposes of this study we define these changes in growth rate inferred from regression as PSFs.

Measurement of soil fertility

Since soil nutrient rates were correlated (Appendix S1: Fig. S1), we used the first component of a principle component analysis as an index of soil fertility and statistical predictor variable. The first principle component explained 78.4% of variance in soil nutrient availability, and was positively correlated with nitrate, phosphorous, potassium, calcium, and magnesium (Appendix S1: Fig. S2). To confirm that there was no correlation between soil fertility and phylogenetic relatedness between the focal and conditioning species we calculated local Moran's I (I_i) on soil fertility for all species from which soils were collected, treating soil fertility as an extended plant trait. Moran's I is a Localized Indicator of Phylogenetic Association (LIPA) and measures local correlation of signal among closely related species in the phylogeny (Keck et al. 2016). This analysis was run for each focal species, to ensure that for no focal species was soil fertility confounded with phylogenetic relatedness to the conditioning species of each soil. We found no significant I_i values for any focal species, in either control or fungicide groups. These tests were implemented using the packages phylobase (R Hackathon et al. 2020) and phylosignal (Keck et al. 2016).

Growth analysis

To assess plant performance across our treatments we calculated the relative growth rate (RGR) of biomass ($mg \cdot g^{-1} \cdot d^{-1}$) for each seedling as $[\log(bm_h) - \log(bm_i)]/d$, where bm_h is biomass at harvest, bm_i is estimated initial biomass at first census (at transplant), and d is the number of days between the initial census and harvest. Initial biomass estimates were predicted from species-specific linear regression models developed using the stem diameter, stem height, and leaf number measured on seedlings harvested at transplant as predictor variables. We selected reduced models for each species using an AIC threshold of 2 and used the resulting preferred models to estimate initial biomass for seedlings in the experiment (adjusted R^2 = 0.32–0.97, Appendix S1: Table S3).

Statistical modeling

We employed a replicated regression-based analysis (sensu Sayago et al. 2004) to measure treatment effects on seedling growth rate using a linear mixed-effects model. RGR of total biomass was the response variable, with mycorrhizal type (AM vs. EM), phylogenetic distance between focal and conditioning species, soil fertility index, and fungicide treatment (control/no-fungicide vs. fungicide) as fixed effects. We retained all higher order interactions among fixed effects, as they were explicitly designed into the experiment to test our hypotheses. Species and experimental block were modeled as random effects with a nested structure (block within species). Support for different random effects models was evaluated using AIC model selection with maximum likelihood estimation, which favored retaining random intercepts and dropping random slopes for both variables. To better evaluate individual species responses to experimental treatments, we also fit separate mixed models for each focal species using the same fixed effect model, but with only experimental block as a random intercept.

All growth models were fit using the package nlme (Pinheiro et al. 2018). Residuals were assessed visually for normality, and heteroscedasticity was assessed using Levene's tests for equality of variances. When necessary, heteroscedasticity of continuous or within-group error was modeled using variance functions in the nlme package, and support for variance weighting was confirmed using AIC. We compared fixed effects estimates across

experimental groups using least squares means to estimate the marginal effect of linear predictors as implemented in the package emmeans (Lenth 2016). To further explore the nature of interactions between phylogenetic distance, mycorrhizal type, and fungicide, we used simple slopes analysis (Cohen et al. 2003, Bauer and Curran 2005) as implemented by reghelper (Hughes 2020). Simple slopes is a form of interaction test for moderated multiple regression models that allows for testing whether the effect of one predictor differs from zero over different ranges or levels of other moderators within the model. We also ran independent models for subsets of data containing only seedlings in the Control or Fungicide treatments.

EM colonization analysis

We analyzed effects of all experimental treatments on percent EM colonization of all EM focal species using a generalized linear mixed model (GLMM) of the number of colonized root tips on a seedling out of 100 sampled. We used the same model structure as for the growth models described in "Growth analysis", except with a negative binomial error distribution. We used a negative binomial because a binomial error distribution was not a good fit to the percent colonization data due to overdispersion, as supported by AIC model selection and the dispersion parameter estimate (Appendix S1: Table S4). Root EM-colonization data were zero-inflated because of a large proportion of uncolonized seedling root systems in one species, *Castanopsis*, in which 51% of seedlings remained uncolonized by EM fungi at the end of the experiment. In contrast, very few seedlings of the four other EM species were uncolonized (0–7.5%), and the mean percentage of seedlings colonized among these species was high (97% ± 1.6%; mean ± SE). We therefore excluded uncolonized seedlings of *Castanopsis* from our colonization model and separately modeled colonization success (whether a seedling was colonized or not) for *Castanopsis* using a GLMM with a binomial error distribution. Removing zero-count data from *Castanopsis* corrected zero-inflation in the overall data set without altering the underlying distribution (Appendix S1: Fig. S3), and the GLMM fit to zero occurrence for *Castanopsis* alone indicated no significant treatment effects on its colonization success (Appendix S1: Table S5). To ensure that the removal of uncolonized *Castanopsis* from the data set did not bias the results of our main colonization model, we compared our results to (1) a model fit after dropping uncolonized seedlings of *all* species and (2) a model fit after dropping all *Castanopsis* data points, both of which yielded nearly identical inference (Appendix S1: Tables S6 and S7).

To assess the effects of EM colonization on seedling RGR, we used a simple linear regression model with EM host species and percent root colonization as interacting fixed effects. All GLMMs were fit using the packages lme4 (Bates et al. 2015) and dispersion parameters were estimated using the package blmeco (Korner-Nievergelt et al. 2015). We compared marginal effects estimates of fixed factors across experimental groups as implemented in the packages emmeans (Lenth 2016) and sjPlot (Lüdecke 2018).

Results

Growth response

Seedling–soil phylogenetic distance affected seedling RGR differently for AM vs. EM species, and this difference was removed by fungicide application (significant mycorrhizal type × phylogenetic distance × fungicide interaction; Table 1, Fig. 2). Without fungicide, RGR of EM seedlings decreased as the phylogenetic distance of the conditioning soil increased, consistent with positive PSF (phylogenetic distance slope = −0.63 ± 0.20; $P = 0.006$ Appendix S1: Table S8). In contrast, for AM seedlings, biomass growth rate increased as phylogenetic distance increased, consistent with negative PSF (phylogenetic distance slope = 0.51 ± 0.48; $P = 0.12$ Appendix S1: Table S8). Slopes for AM and EM differed significantly from each other in control treatments (mycorrhizal type × phylogenetic distance $P = 0.018$; Appendix S1: Table S9). By contrast, among fungicide-treated seedlings, phylogenetic distance did not significantly affect the biomass growth rate of seedlings of either mycorrhizal type (EM phylogenetic distance slope = −0.16 ± 0.29; $P = 0.619$, AM phylogenetic distance slope = −0.24 ± 0.33; $P = 0.636$ Appendix S1: Table S8), nor did AM or EM differ from each other (mycorrhizal type × phylogenetic distance = 0.827; Appendix S1: Table S9). The impact of phylogenetic distance also varied with soil fertility, depending on mycorrhizal type (significant mycorrhizal type × soil fertility × phylogenetic distance interaction; Table 1, Fig. 3). While variation in biomass growth of AM seedlings with phylogenetic distance tended to be more consistent with negative PSF as soil fertility increased, for EM seedlings the growth-phylogenetic distance relationship did not depend on soil fertility.

In the all-species model of biomass growth, the random effects model incorporating species and experimental block accounted for most of the explained variation in growth rate, whereas fixed effects accounted for only 2% (marginal R^2 of 54% vs. conditional R^2 of 56%). For individual species models, effect sizes for experimental treatments differed greatly among species (Appendix S1: Table S10), and the variance explained by fixed effects ranged from marginal $R^2 < 0.1\%$ (*Castanopsis*) to marginal-$R^2 = 14\%$ (*S. scaberrima*), with seedling-soil phylogenetic distance accounting for <0.1% (*Madhuca*) to 10% (*S. scaberrima*). In two species, second-order interactions explained more variance than all main treatment effects combined (*Dacryodes*, *Dryobalanops*).

TABLE 1. Treatment effects on seedling biomass growth rate based on linear mixed model ANCOVA using fixed effects of host mycorrhizal type (AM or EM), soil fertility, seedling-soil phylogenetic distance, and fungicide application with random effects of focal species and experimental block.

Treatment effects	χ^2	df	*P*	Variance	SD
Fixed effects					
Mycorrhizal type	0.137	1	0.711		
Soil fertility	0.792	1	0.374		
Phylogenetic distance	4.591	1	0.032		
Fungicide	1.113	1	0.291		
Mycorrhizal type × Soil fertility	3.692	1	0.055		
Mycorrhizal type × Phylogenetic distance	3.028	1	0.082		
Soil fertility × Phylogenetic distance	2.682	1	0.101		
Mycorrhizal type × Fungicide	0.403	1	0.525		
Soil fertility × Fungicide	0.489	1	0.484		
Phylogenetic distance × Fungicide	0.019	1	0.889		
Mycorrhizal type × Soil fertility × Phylogenetic distance	4.502	1	0.034		
Mycorrhizal type × Soil fertility × Fungicide	1.380	1	0.240		
Mycorrhizal type × Phylogenetic distance: Fungicide	4.180	1	0.041		
Soil fertility × Phylogenetic distance × Fungicide	1.089	1	0.297		
Mycorrhizal type × Soil fertility × Phylogenetic distance × Fungicide	0.034	1	0.853		
Random effects					
Focal species				1.479	1.216
Block				0.228	0.477

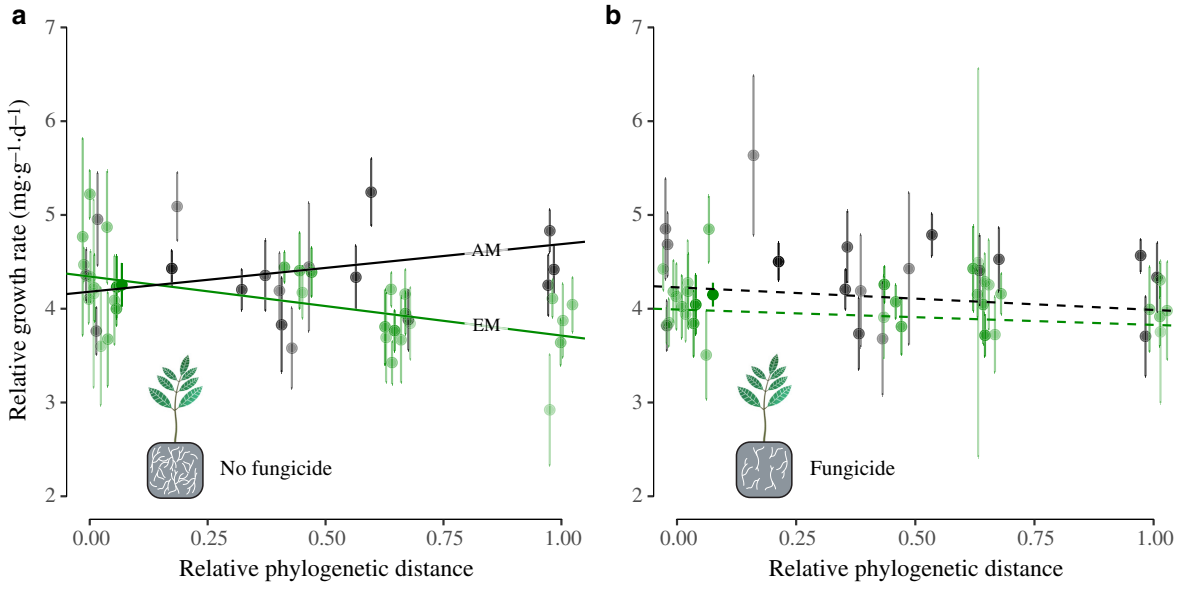

FIG. 2. Plant–soil phylogenetic distance effect on plant growth across mycorrhizal types in (a) control and (b) fungicide groups. The arbuscular mycorrhizal (AM) group is shown in black and the ectomycorrhizal (EM) group in green. Trend lines indicate the model estimated marginal effect of seedling–soil phylogenetic distance for fungicide and control groups; solid lines indicate estimates not overlapping zero, while dashed lines indicate estimates overlapping zero. For visualization purposes only, data are summarized as the within-species by phylogenetic distance mean ± SE to improve readability and adjust for random effects; point intensity indicates the number of observations within each summary point (range = 3–27). Mycorrhizal type × phylogenetic distance × fungicide treatment interaction P = 0.041. Trend lines estimate marginal effects at intermediate fertility.

Ectomycorrhizal colonization

We found that, in EM seedlings, all three main effects of soil fertility, phylogenetic distance, and fungicide application significantly affected the percent EM colonization of seedling root systems (Appendix S1: Table S11). Fungicide application significantly decreased colonization by EM fungi ($\chi^2 = 19.29$, df = 1, $P < 0.001$) from 39.5% ± 1.6% to 33.3% ± 1.4%, a roughly 15% reduction (Fig. 4c), suggesting that fungicide treatment had direct effects on root-associated fungi. Increasing seedling–soil phylogenetic distance also

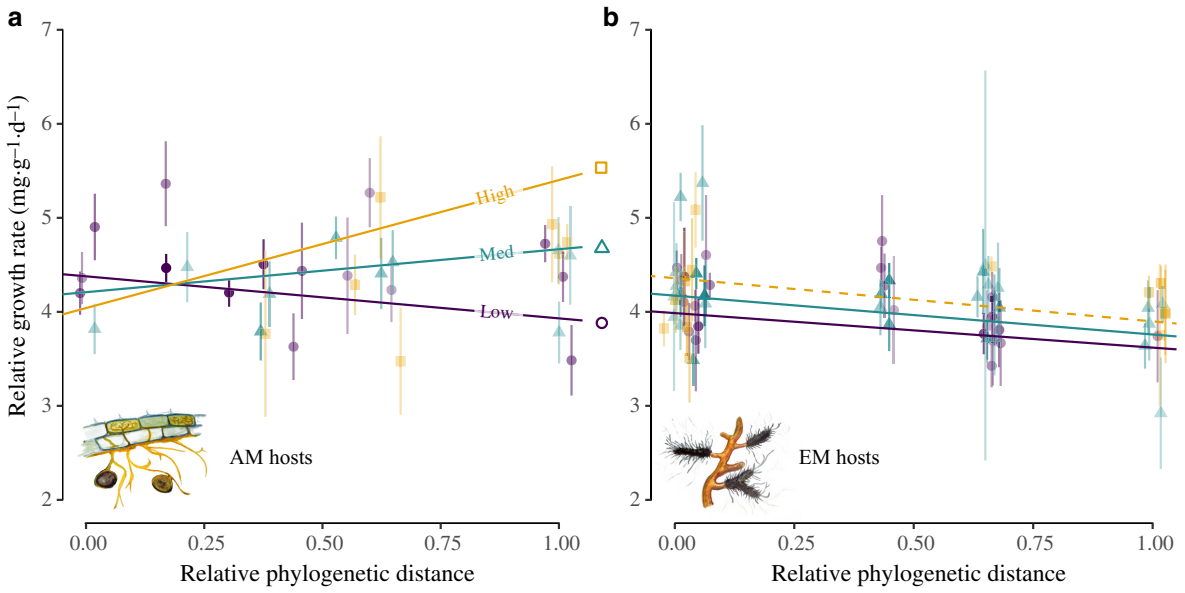

FIG. 3. Plant–soil phylogenetic distance effect on seedling growth estimated at different soil fertility levels in (a) AM and (b) EM groups. Purple circle, blue triangle, and yellow squares indicate low, intermediate, and high intervals of soil fertility. Trend lines indicate the model estimated marginal effect of seedling–soil phylogenetic distance estimated at three levels of soil fertility; solid lines indicate estimates not overlapping zero, while dashed lines indicate estimates overlapping zero. For visualization purposes only and to facilitate interpretation of the continuous interaction term, data are binned over three soil fertility intervals and summarized as the within species × phylogenetic distance mean ± SE and have been adjusted for random effects; transparency indicates observations within each summary point (range = 3–37). Mycorrhizal type × soil fertility × phylogenetic distance interaction $P = 0.034$. Data and trend lines are averaged over both fungicide and control groups.

significantly reduced root fungal colonization in EM hosts ($\chi^2 = 9.37$, df = 1, $P = 0.002$; Fig. 4a). Increased soil fertility was associated with greater colonization ($\chi^2 = 18.62$, df = 1, $P < 0.001$), and this effect was more pronounced in control seedlings than those that received fungicide (interaction $\chi^2 = 10.12$, df = 1, $P = 0.001$; Fig. 4b). Colonization by EM fungi was also significantly associated with faster biomass growth rate ($F_{1, 599} = 55.27$, $P < 0.001$), an effect that was consistent across species (interaction $F_{4, 599} = 0.5325$, $P = 0.71$) (Fig. 5). In species-specific tests, the correlation between root colonization and growth varied substantially and was significant for all species except *Castanopsis* (*Castanopsis* $r = 0.17$, df = 59, $P = 0.186$; *Dryobalanops* $r = 0.25$, df = 145, $P = 0.002$; *S. curtisii* $r = 0.47$, $P < 0.001$; *S. laxa* $r = 0.20$; $P = 0.014$, *S. scaberrima* $r = 0.27$, $P = 0.030$).

DISCUSSION

Among other hypotheses, negative plant soil feedbacks (PSFs) have emerged as a potential mechanism thought to promote coexistence in high diversity plant communities through the strong effects of species-specific pathogens (Augspurger and Wilkinson 2007, Bagchi et al. 2010*b*, 2014). Despite recognition of the effects of EM fungi on both PSF (Bennett et al. 2017, Teste et al. 2017) and critical soil processes (Clemmensen et al. 2013, Phillips et al. 2013, Averill et al. 2014, Terrer et al. 2016), there are few studies of tropical PSF outside of AM-dominated neotropical forests. To address these knowledge gaps, we used a manipulative experiment with seedlings of eight tree species to investigate sources of variation in plant–microbe interactions in a high diversity, codominant AM–EM rain forest in Borneo. Our results show that early seedling growth in this forest is influenced in predictable ways by adult tree conditioning of the soil microbial community. Moreover, we found that the strength and direction of these growth effects depend on a tree species' mycorrhizal association, local soil nutrient availability, and the phylogenetic relatedness of the overstory tree species.

The strength of conspecific negative density dependence (CNDD) and PSF experienced by tropical tree species is often interpreted as primarily a function of susceptibility to species-specific natural enemies. However, our results add to growing evidence that PSFs are more complicated than this (De Long et al. 2018). We reason that dispersing seeds encounter a spatially heterogeneous landscape of microbes that influence their growth across the forest floor. The resulting heterogeneity in seedling growth and mortality stem directly from negative interactions with natural enemies, but also from the evolutionary history of plants with fungal mutualists, and how soil resource availability affects these resource-trading relationships. Theoretical models suggest that the size of the tree species pool combined with differences in the benefits conferred by AM vs. EM fungi to

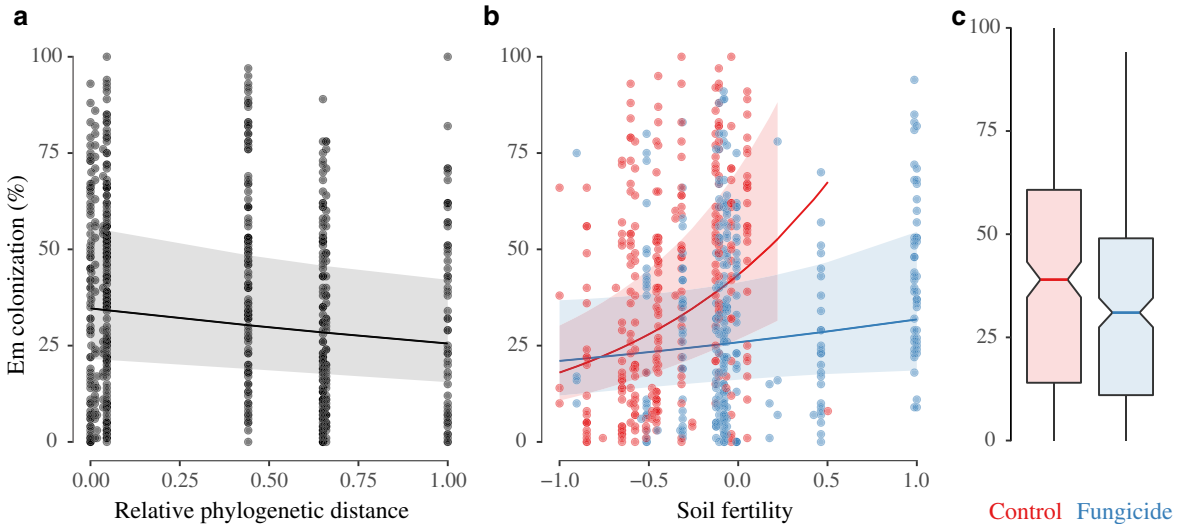

FIG. 4. Treatment effects on seedling root colonization by EMF. In panels b and c, control treatments are represented in red, while fungicide treatments are represented in blue. Trend lines in panels a and b indicate generalized mixed model predictions of root colonization and shaded regions indicate 95% confidence intervals.

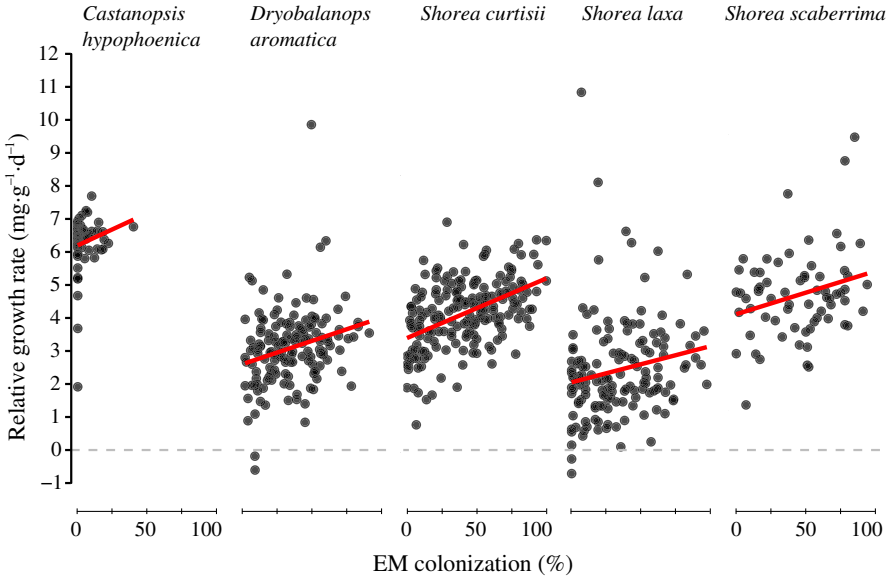

FIG. 5. Seedling root colonization by EMF is positively associated with seedling growth rate across all EM species. Lines indicate linear model fits for each species.

their hosts affect the probability of tree species' rising to competitive dominance (Fukami et al. 2017). Yet, how the complexities that we have discovered in the drivers of PSF enhance the diversity-maintaining mechanism of CNDD vs. promoting dominance of tree taxa with particular mycorrhizal associations across environmentally heterogeneous landscapes requires further exploration.

The regional dominance of species in a single tree family, the Dipterocarpaceae, in Southeast Asian forests (Alexander and Hogberg 1986), as well as the capacity of some EM host species to form monodominant stands in otherwise high-diversity tropical rain forests (Connell and Lowman 1989, Torti et al. 2001) have defied convincing explanation. One hypothesis is that, in contrast to AM host species, EM host species have less negative or even positive PSFs, and that EM PSFs become more positive in soils conditioned by closely related species, which would ultimately act to generate a positive feedback for recruitment of EM host species from the same evolutionary lineage at larger spatial scales (Fukami et al. 2017). Consistent with this hypothesis, we demonstrate that seedlings of EM species, particularly those of the Dipterocarpaceae, experience more positive effects from host-specific soil microbes and that, based on the

results from our fungicide treatment, association with fungal mutualists likely underlies these effects. We also found that seedlings of AM tree species experienced more negative effects of host specific microbes and that the effect of growing under soils conditioned by close relatives was opposite to EM host species. The suite of possible drivers of such PSFs should be the same across all forests, but as we have demonstrated here, the relative strength, direction, and phylogenetic influence of PSF can differ across mycorrhizal types and soil environments in a species-rich tropical forest. Results from our study generalize the findings from temperate forests that show corresponding patterns of more positive PSF for EM tree species (Bennett et al. 2017), as well as a recent field study from subtropical Asia showing that soil accumulation of EM fungi reduces conspecific negative density dependence (Chen et al. 2019). Beyond this, our results suggest that there are important differences across major tropical regions in the nature of PSFs depending on the composition of the local species pool and geological history.

Mycorrhizal variation in feedback effects

There is increasing evidence that the abundance and distribution of EM host species can affect forest diversity and ecosystem functions, such as corresponding carbon storage, nutrient cycling, and responses to anthropogenic change (Averill et al. 2014, Terrer et al. 2016, Bennett et al. 2017). Previous work in temperate North America has indicated that EM and AM tree species may experience different plant–soil feedbacks, with EM and AM taxa experiencing conspecific facilitation and inhibition, respectively (Bennett et al. 2017). Given the substantial differences in climate, soil environment, and biotic assemblages, it was unclear whether similar patterns would also be observed in tropical ecosystems, but our findings are consistent with those from temperate forests and extend them by showing variation between AM and EM host species in the effect of phylogenetic relatedness on PSF. For seedlings of EM trees, slower growth in soil collected from under distantly related tree species likely results from reduced availability or compatibility of EM fungal inoculum in soil and thus reduced root colonization by these mutualists, as in our experiment. While previous work in this forest has shown that interactions between EM fungi and Dipterocarpaceae may not show strict host specificity among confamilial species (Peay et al. 2015), our results here suggest that host preferences exist that can improve colonization and benefits for seedlings growing beneath conspecifics or close relatives, leading to positive PSFs. The beneficial effects we observed could also stem from reduced pathogen infection, as EM fungi can increase disease resistance, including via direct antagonism with soil fungal pathogens (Marx 1972, Chakravarty and Unestam 1987, Lie et al. 1995). Thus, while all seedlings likely confront greater abundance of pathogens to which they are susceptible when growing near close relatives, our results suggest that such negative effects could be more strongly ameliorated in EM vs. AM hosts by improved growth resulting from greater EMF colonization, more favorable resource-trading relationships, and reduced infection by or impacts of pathogens (Bennett et al. 2017).

In contrast, we show the opposite pattern in AM hosts: faster growth in soil collected from beneath distantly related tree species, which could arise through several mechanisms. Since closely related plant species tend to share pathogens, this phylogenetic PSF could be mediated by escape from natural enemies of near relatives (Gilbert and Webb 2007, Liu et al. 2011). Since AM fungi are generally broader in host range than EM fungi (Davison et al. 2015), seedlings of AM host species are less likely to lose the benefit of mutualists when growing under more distantly related tree species. Indeed, because of variation along the mutualism–parasitism continuum (Bronstein 1994), AM fungi conferring minimal benefits to plants can dominate locally and themselves cause negative feedbacks (Bever 2002). Dissecting how the interactions with pathogens and mutualists differ between AM and EM host species to produce the variation in PSFs that we observed would be aided by genomic evidence identifying the microbial colonists of these seedlings' roots.

Within mycorrhizal types, individual species were also a significant source of variation in PSF strength. This is not surprising, given the individual variation in growth rates between species, and given that variation in PSF within mycorrhizal types has been documented in the temperate biome as well (Bennett et al. 2017). This interspecific variability has ecological consequences, but also highlights the importance of testing multiple species in PSF experiments, especially given that major effects were sometimes not detectable with the reduced power of single species models.

Interactive effects of biotic feedback and resource availability

Ecological theory and empirical evidence indicate that resource availability can strongly influence species interactions and may shift crucial balance points for interactions that exist along a mutualism–parasitism continuum, including those between plants and mycorrhizal fungi (Johnson et al. 1997). Resource availability has been found to affect both CNDD and PSF, with stronger CNDD associated with greater soil resource availability (LaManna et al. 2016) and more negative PSF associated with increased light availability (Smith and Reynolds 2015) in temperate forests. Consistent with this, we found that among AM host species, greater soil resource availability was associated with more negative PSFs. Johnson et al. (2010) also found that AM fungi of temperate grass species became less beneficial as soil fertility increased. Among EM tree species, however, we

found that soil fertility had no effect on PSF. While the mechanisms controlling resource trading relationships between plants and EM fungi are poorly understood (Bogar et al. 2019), our finding is consistent with the view that, compared to AM, EM associations are more beneficial to plants (Bennett et al. 2017) but see (Karst et al. 2008) and have greater plant control (Nehls et al. 2007). Alternatively, EM fungal communities may simply have greater functionality that provides stable benefits across a larger range of soil conditions. In support of this idea, a recent study showed that tropical EM-associated seedlings assimilated P in a broader range of chemical forms than AM-associated seedlings (Liu et al. 2018). Interestingly, Chen et al. (2019) also showed that accumulation of EM fungi in the soil could also benefit AM host trees, and suggested that AM trees may benefit from modifying soil conditions to promote EM abundance. All soils in our study site are relatively nutrient depleted (Baillie et al. 2006), so it is possible that different outcomes would have been observed at the high nitrogen levels that have been shown in temperate forests to disrupt EM symbiosis (van der Linde et al. 2018).

Biogeographic variation in PSF

Our findings that EM trees experience positive effects of host specific microbes may help explain some of the biogeographic differences among tropical rainforests. Average CNDD has been observed to be strongest in species rich communities and at lower latitudes (Johnson et al. 2012), an effect that is often attributed to more negative effects of pathogenic fungi nearer the equator (Bagchi et al. 2014, Bennett et al. 2017). In neotropical forests, where the Janzen-Connell hypothesis was first developed, negative PSFs appear to predominate (Mangan et al. 2010*b*). While we observed some negative PSFs for AM host species, PSFs varied strongly by mycorrhizal type and soil fertility, raising questions about the generality of negative PSFs and whether they are the dominant process maintaining species diversity in tropical tree communities. While the monospecific dominance of EM hosts observed in some neotropical forests is associated with a positive home soil advantage (McGuire 2007, Corrales et al. 2016), we show that net positive effects of home soil microbes exist in a tropical forest in which a high diversity of both EM and AM host species coexist. This positive phylogenetic feedback may explain some of the unique features of SE Asian forests, such as the familial dominance of the Dipterocarpaceae. Similarly, tree species distributions in dipterocarp forests are more spatially aggregated than in non-dipterocarp forests (Condit et al. 2000). Such greater spatial aggregation could arise from limited dispersal, but only in combination with weak CNDD (Russo and Augspurger 2004), which our results show could be mediated by more positive PSFs for EM host species. However, it is unclear why some systems exhibit monospecific dominance of EM host species, whereas others exhibit coexistence of AM and EM species at comparable levels of richness. Fukami et al. (2017) developed a non-phylogenetic PSF model showing that such variation can arise due to differences in trait characteristics of regional species pools that would be promising to follow up with future empirical studies.

Conclusions

In this highly diverse Bornean rain forest, we demonstrate that host mycorrhizal association interacts with soil fertility to produce a diversity of outcomes in the interactions between seedlings and host specific microbes. Because the distribution of host specific microbes will also vary depending on the evolutionary history of the overstory trees, seeds dispersed in this forest experience a complex landscape of plant–microbe interactions that likely influence spatial patterns of recruitment. To the extent that interactions between plants and soil microbes contribute to CNDD, they must influence diversity in plant communities (Mills and Bever 1998, Johnson et al. 2012). Negative PSF is often viewed as a primary driver of CNDD in species-rich tropical forests (Mangan et al. 2010*b*), but the positive and variable PSF that we found in a diverse tropical forest here may help explain biogeographic differences in forest structure across tropical rainforests. Our findings also call for greater investigation into the generality of negative PSF in maintaining tropical tree diversity.

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Literature Cited

Alexander, I. J., and P. Hogberg. 1986. Ectomycorrhizas of tropical angiospermous trees. New Phytologist 102:541–549.

Augspurger, C. K. 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. Journal of Ecology 71:759–771.

Augspurger, C. K., and H. T. Wilkinson. 2007. Host specificity of pathogenic pythium species: implications for tree species diversity. Biotropica 39:702–708.

Averill, C., B. L. Turner, and A. C. Finzi. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. Nature 505:543–545.

Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T. Lewis. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature 506:85–88.

Bagchi, R., M. C. Press, and J. D. Scholes. 2010*a*. Evolutionary history and distance dependence control survival of dipterocarp seedlings. Ecology Letters 13:51–59.

Bagchi, R., T. Swinfield, R. E. Gallery, O. T. Lewis, S. Gripenberg, L. Narayan, and R. P. Freckleton. 2010*b*. Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. Ecology Letters 13:1262–1269.

Baillie, I. C., P. S. Ashton, S. P. Chin, S. J. Davies, P. A. Palmiotto, S. E. Russo, and S. Tan. 2006. Spatial associations of humus, nutrients and soils in mixed dipterocarp forest at Lambir, Sarawak, Malaysian Borneo. Journal of Tropical Ecology 22:543–553.

Barberá, C. 1989. Pesticidas Agrícolas. Omega, Barcelona, Spain.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bauer, D. J., and P. J. Curran. 2005. Probing interactions in fixed and multilevel regression: inferential and graphical techniques. Multivariate Behavioral Research 40:373–400.

Bennett, J. A., H. Maherali, K. O. Reinhart, Y. Lekberg, M. M. Hart, and J. N. Klironomos. 2017. Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. Science 355:181–184.

Bever, J. D. 2002. Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. Proceedings of the Royal Society B 269:2595–2601.

Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. Journal of Ecology 85:561–573.

Bogar, L., K. Peay, A. Kornfeld, J. Huggins, S. Hortal, I. Anderson, and P. Kennedy. 2019. Plant-mediated partner discrimination in ectomycorrhizal mutualisms. Mycorrhiza 29: 97–111.

Brearley, F. Q. 2012. Ectomycorrhizal associations of the Dipterocarpaceae. Biotropica 44:637–648.

Bronstein, J. L. 1994. Conditional outcomes in mutualistic interactions. Trends in Ecology & Evolution 9:214–217.

Bruns, T. D., M. I. Bidartondo, and D. L. Taylor. 2002. Host specificity in ectomycorrhizal communities: what do the exceptions tell us? Integrative and Comparative Biology 42:352–359.

Bruns, T. D., and R. P. Shefferson. 2004. Evolutionary studies of ectomycorrhizal fungi: recent advances and future directions. Canadian Journal of Botany 82:1122–1132.

Chakravarty, P., and T. Unestam. 1987. Differential influence of ectomycorrhizae on plant growth and disease resistance in *Pinus sylvestris* seedlings. Journal of Phytopathology 120:104–120.

Chen, L., N. G. Swenson, N. Ji, X. Mi, H. Ren, L. Guo, and K. Ma. 2019. Differential soil fungus accumulation and density dependence of trees in a subtropical forest. Science 366:124–128.

Clemmensen, K. E., A. Bahr, O. Ovaskainen, A. Dahlberg, A. Ekblad, H. Wallander, J. Stenlid, R. D. Finlay, D. A. Wardle, and B. D. Lindahl. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339:1615–1618.

Cohen, J., P. Cohen, S. G. West, and L. S. Aiken. 2003. Applied multiple regression/correlation analyses for the behavioral sciences. Third edition. Lawrence Erlbaum Associates, Mahwah, New Jersey, USA.

Cohen, Y., and M. D. Coffey. 1986. Systemic fungicides and the control of oomycetes. Annual Review of Phytopathology 24:311–338.

Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. Science 329:330–332.

Condit, R., et al. 2000. Spatial patterns in the distribution of tropical tree species. Science 288:1414–1418.

Condit, R., S. P. Hubbell, and R. B. Foster. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a Neotropical forest. American Naturalist 140:261–286.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of Populations 298:312.

Connell, J. H., and M. D. Lowman. 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. American Naturalist 134:88–119.

Corrales, A., S. A. Mangan, B. L. Turner, and J. W. Dalling. 2016. An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. Ecology Letters 19:383–392.

Davies, S. J., S. Tan, J. V. LaFrankie, and M. D. Potts. 2005. Soil-related floristic variation in a hyperdiverse dipterocarp forest. Pages 22–34 *in* D. Roubik, S. Sakai, and A. A. Hamid editors.Pollination ecology and the rain forest. Springer-Verlag, New York, New York, USA.

Davison, J., et al. 2015. Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. Science 349:970–973.

De Long, J. R., E. L. Fry, G. F. Veen, and P. Kardol. 2018. Why are plant–soil feedbacks so unpredictable, and what to do about it? Functional Ecology 33:118–128.

Duhamel, M., J. Wan, L. M. Bogar, R. M. Segnitz, N. C. Duncritts, and K. G. Peay. 2019. Plant selection initiates alternative succesional trajectories in soil microbial community after disturbance. Ecological Monographs 89:1–28.

Fukami, T., M. Nakajima, C. Fortunel, P. V. A. Fine, C. Baraloto, S. E. Russo, and K. G. Peay. 2017. Geographical variation in community divergence: insights from tropical forest monodominance by ectomycorrhizal trees. American Naturalist 190:S105–S122.

Gilbert, G. S. 2002. Evolutionary ecology of plant diseases in natural ecosystems. Phytopathology 40:13–43.

Gilbert, G. S., and C. O. Webb. 2007. Phylogenetic signal in plant pathogen-host range. Proceedings of the National Academy of Sciences USA 104:4979–4983.

Gundale, M. J., D. A. Wardle, P. Kardol, and M. C. Nilsson. 2019. Comparison of plant-soil feedback experimental approaches for testing soil biotic interactions among ecosystems. New Phytologist 221:577–587.

Hoeksema, J. D., et al. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecology Letters 13:394–407.

Hughes, J. 2020. reghelper: Helper Functions for Regression Analysis. https://CRAN.R-project.org/package=reghelper

Ishida, T. A., K. Nara, and T. Hogetsu. 2007. Host effects on ectomycorrhizal fungal communities: insight from eight host species in mixed conifer–broadleaf forests. New Phytologist 174:430–440.

Janos, D. P. 1980. Mycorrhizae influence tropical succession. Biotropica 12:56–64.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

Johnson, D. J., W. T. Beaulieu, J. D. Bever, and K. Clay. 2012. Conspecific negative density dependence and forest diversity. Science 336:904–907.

Johnson, N. C., J. H. Graham, and F. A. Smith. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytologist 135:575–586.

Johnson, N. C., G. W. T. Wilson, M. A. Bowker, J. A. Wilson, and R. M. Miller. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. Proceedings of the National Academy of Sciences USA 107:2093–2098.

Karst, J., L. Marczak, M. D. Jones, and R. Turkington. 2008. The mutualism-parasitism continuum in ectomycorrhizas: a quantitative assessment using meta-analysis. Ecology 89: 1032–1042.

Keck, F., F. Rimet, A. Bouchez, and A. Franc. 2016. phylosignal: an R package to measure, test, and explore the phylogenetic signal. Ecology and Evolution 6:2774–2780.

Kivlin, S. N., R. Bedoya, and C. V. Hawkes. 2018. Heterogeneity in arbuscular mycorrhizal fungal communities may contribute to inconsistent plant-soil feedback in a Neotropical forest. Plant and Soil 432:29–44.

Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417: 67–70.

Korner-Nievergelt, F., T. Roth, S. Von Felten, and J. Guélat. 2015. Bayesian data analysis in ecology using linear models with R, BUGS, and Stan. Academic Press, San Diego, California, USA.

LaManna, J. A., M. L. Walton, B. L. Turner, and J. A. Myers. 2016. Negative density dependence is stronger in resource-rich environments and diversifies communities when stronger for common but not rare species. Ecology Letters 19: 657–667.

Lee, H. S., S. J. Davies, J. V. LaFrankie, S. Tan, and T. Yamakura. 2002. Floristic and structural diversity of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. Oikos 14:379–400.

Lei, Z. P., J. R. Jin, and C. W. Wang. 1995. Antagonism between ectomycorrhizal fungi and plant pathogens. Pages 77–81 in M. C. Brundett, M. B. Dell and N. Malajczuk, editors. Mycorrhizas for plantation forestry in Asia. Australian Centre for International Agricultural Research, Kaiping, China. Proceedings of an International Symposium and Workshop, 7–11 November 1994, Kaiping, China. Australian Centre for International Agricultural Research, Proceedings No. 62, Canberra, Australia.

Lenth, R. V. 2016. Least-squares means: The RPackage lsmeans. Journal of Statistical Software 69:1–33.

Lindahl, B. D., and A. Tunlid. 2014. Ectomycorrhizal fungi – potential organic matter decomposers, yet not saprotrophs. New Phytologist 205:1443–1447.

Liu, X., D. F. R. P. Burslem, J. D. Taylor, A. F. S. Taylor, E. Khoo, N. M. Lee, T. Helgason, and D. Johnson. 2018. Partitioning of soil phosphorus among arbuscular and ectomycorrhizal trees in tropical and subtropical forests. Ecology Letters 21:713–723.

Liu, X., M. Liang, R. S. Etienne, Y. Wang, C. Staehelin, and S. Yu. 2011. Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest. Ecology Letters 15: 111–118.

Liu, Y., S. Fang, P. Chesson, and F. He. 2015. The effect of soil-borne pathogens depends on the abundance of host tree species. Nature Communications 6:10017.

Lüdecke, D.2018. sjPlot: Data Visualization for Statistics in Social Science. R package version 3.1-137. http://doi.org/10.5281/zenodo.1308157

Mangan, S. A., E. A. Herre, and J. D. Bever. 2010*a*. Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant–soil feedback. Ecology 91:2594–2603.

Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever. 2010*b*. Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. Nature 466:752–755.

Martınez-Toledo, M. V., V. Salmeron, B. Rodelas, C. Pozo, and J. González-López. 1998. Effects of the fungicide Captan on some functional groups of soil microflora. Soil Biology and Biochemistry 7:245–255.

Marx, D. H. 1972. Ectomycorrhizae as biological deterrents to pathogenic root infections. Phytopathology 10:429–454.

McGuire, K. L. 2007. Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology 88:567–574.

Mills, K. E., and J. D. Bever. 1998. Maintenance of diversity within plant communities: soil pathogens as agents of negative feedback. Ecology 79:1595–1601.

Morris, W. F., et al. 2007. Direct and interactive effects of enemies and mutualists on plant performance: a meta-analysis. Ecology 88:1021–1029.

Nara, K. 2006. Ectomycorrhizal networks and seedling establishment during early primary succession. New Phytologist 169:169–178.

Nehls, U., N. Grunze, M. Willmann, M. Reich, and H. Küster. 2007. Sugar for my honey: carbohydrate partitioning in ectomycorrhizal symbiosis. Phytochemistry 68:82–91.

Peay, K. G., S. E. Russo, K. L. McGuire, Z. Lim, J. P. Chan, S. Tan, and S. J. Davies. 2015. Lack of host specificity leads to independent assortment of dipterocarps and ectomycorrhizal fungi across a soil fertility gradient. Ecology Letters 18:807–816.

Pellitier, P. T., and D. R. Zak. 2017. Ectomycorrhizal fungi and the enzymatic liberation of nitrogen from soil organic matter: why evolutionary history matters. New Phytologist 217:68–73.

Phillips, R. P., E. Brzostek, and M. G. Midgley. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. New Phytologist 199:41–51.

Pinheiro, J., D. Bates, S. DebRoy, and R Core Team. 2018. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137. https://CRAN.R-project.org/package=nlme

Proctor, J., J. M. Anderson, P. Chai, and H. W. Vallack. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak: I. Forest environment, structure and floristics. Journal of Ecology 71:237–260.

R Hackathon, et al. 2020. phylobase: Base package for phylogenetic structures and comparative data. R package version 0.8.10. https://CRAN.R-project.org/package=phylobase

Read, D. J., and J. Perez-Moreno. 2003. Mycorrhizas and nutrient cycling in ecosystems—A journey towards relevance? New Phytologist 157:475–492.

Reinhart, K. O., and M. J. Rinella. 2016. A common soil handling technique can generate incorrect estimates of soil biota effects on plants. New Phytologist 210:786–789.

Rinella, M. J., and K. O. Reinhart. 2017. Mixing soil samples across experimental units ignores uncertainty and generates incorrect estimates of soil biota effects on plants. New Phytologist 216:15–17.

Russo, S. E., and C. K. Augspurger. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecology Letters 7:1058–1067.

Russo, S. E., S. J. Davies, D. A. King, and S. Tan. 2005. Soil-related performance variation and distributions of tree species in a Bornean rain forest. Journal of Ecology 93:879–889.

Sayago, A., M. Boccio, and A. Asuero. 2004. Fitting straight lines with replicated observations by linear regression: the least squares postulates. Critical Reviews in Analytical Chemistry 34:39–50.

Smith, L. M., and H. L. Reynolds. 2015. Plant-soil feedbacks shift from negative to positive with decreasing light in forest understory species. Ecology 96:2523–2532.

Steidinger, B. S., et al. 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. Nature 569:1–12.

Stump, S. M., and L. S. Comita. 2018. Interspecific variation in conspecific negative density dependence can make species less likely to coexist. Ecology Letters 21:1541–1551.

Terrer, C., S. Vicca, B. A. Hungate, R. P. Phillips, and I. C. Prentice. 2016. Mycorrhizal association as a primary control of the CO_2 fertilization effect. Science 353:72–74.

Teste, F., P. Kardol, B. Turner, D. Wardle, G. Zemunik, M. Renton, and E. Laliberte. 2017. Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. Science 355:173–176.

Torti, S. D., P. D. Coley, and D. P. Janos. 1997. Vesicular-arbuscular mycorrhizae in two tropical monodominant trees. Journal of Tropical Ecology 13:623–629.

Torti, S. D., P. D. Coley, and T. A. Kursar. 2001. Causes and consequences of monodominance in tropical lowland forests. American Naturalist 157:141–153.

van der Heijden, M. G. A., T. Boller, and A. Wiemken. 1998. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79:2082–2091.

van der Linde, S., et al. 2018. Environment and host as large-scale controls of ectomycorrhizal fungi. Nature 558:243–248.

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